

Megadisturbances and ecological recovery in the intertidal zone: the role of interspecific competition between bioengineer mussel species

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ABSTRACT: The mega-earthquake that occurred in 2010 in central southern Chile produced a coastal uplift of over 3 m in some areas, resulting in the mass mortality of intertidal organisms. At Punta Hualpen, local extinctions of the 2 intertidal bioengineer mussel species *Perumytilus purpuratus* and *Semimytilus algosus* occurred as a result of the earthquake. Here we evaluate the ecological recovery capacity of these 2 mussels and explore whether differences in their interspecific competitive abilities may explain the restoration of the vertical distribution of these species during the recovery process. A yearly record of abundance of *P. purpuratus* and *S. algosus* in the intertidal zone between 2009 and 2013 indicated that the earthquake had a strong negative impact but that there was a rapid recuperation of the abundance and distributional range of both species over time. Experimental plots in the mid intertidal zone and laboratory experiments showed that *S. algosus* exhibited lower survival and growth rates in the presence of *P. purpuratus*. In addition, our results suggest that the recovery of the vertical distributional pattern of intertidal mussel species may be explained by a combination of interference competition caused by crowding behavior at smaller body sizes and competition due to clearance rate efficiency at larger sizes. However, most research has been focused on the description of the effects of mega-scale natural perturbations on marine communities, instead of trying to understand the underlying mechanisms operating in the recovery process.

KEY WORDS: *Perumytilus purpuratus* · *Semimytilus algosus* · Earthquake · Intertidal community · Ecological resilience · Chilean coast

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INTRODUCTION

Large-scale natural disturbances may have profound impacts on natural ecosystems, affecting many ecological and fitness traits of species through the reduction in species abundance and the destruction of habitat. One of the main issues in ecology is determining the factors and mechanisms driving the ecological recovery of impacted ecosystems (Holling 1973, Thrush et al. 2009). Large-scale natural disturbances such as tsunamis, earthquakes and hurricanes have been viewed as key factors driving the long-term variation in the abundance and distribution of species, diversity, community dynamics and

ecosystem processes in marine systems (Castilla 1988, Gardner et al. 2005, Crabbe et al. 2008, Castilla et al. 2010, Vargas et al. 2011, Jaramillo et al. 2012). However, most research has been focused on the description of the effects of mega-scale natural perturbations and the recovery process, instead of trying to understand the mechanisms underlying this process. Moreover, an understanding of how ecosystems respond to mega-scale natural perturbations, both spatially and temporally, is of utmost importance for management and conservation policies, as well as for establishing mitigation programs.

The high complexity of marine ecological systems, given their specific evolutionary and adaptive char-

acteristics as well as their cross-scale nature, makes predictability in terms of trajectory and time very difficult (Chase 2007, deYoung et al. 2008, Kreyling et al. 2011, Zhou et al. 2014). For instance, life history characteristics of organisms and biological interactions between species should play an important role in the recovery process of natural systems after a perturbation (e.g. Ponge 2013). For example, after local extinction, the dispersal potential of keystone species should determine the speed of recolonization and community recovery (i.e. Thistle 1981, Commito et al. 1995, Shull 1997). Once species arrive, biological interactions such as interspecific competition may drive temporal successional and recovery processes in the community (e.g. Connell 1961, Harger 1968, Dayton 1971, Menge & Sutherland 1976). Thus, field and laboratory experiments under real scenarios need to be conducted to dissect the main factors that determine ecological recovery and are of the utmost importance for advancing our understanding of the response of natural system to perturbations.

Rocky intertidal zones are dominated by sessile and sedentary organisms forming, in some cases, dense aggregations (e.g. Seed 1996, Castilla et al. 2004, Prado & Castilla 2006, Kelaher et al. 2007). These species may act as bioengineer species providing complex matrix habitats for diverse invertebrate assemblages, increasing richness and diversity, and determining intertidal community structure (Castilla et al. 2004, Prado & Castilla 2006, Borthagaray & Carranza 2007, Palomo et al. 2007, Arribas et al. 2013, 2014). Local perturbations, such as storms or strong waves, may produce patches of bare rock within these aggregations. Field observations suggest that early recolonization of small patches should mainly be mediated by intraspecific or interspecific facilitation mechanisms favoring recruitment, growth and survival of species (Littorin & Gilek 1999, Alvarado et al. 2001). However, once the succession process reaches an advanced stage, differences in competitive abilities between species should determine species distribution patterns in this zone and should also explain the temporal evolution of the community (e.g. Connell 1961, Dayton 1971, Griffiths et al. 1992, Tokeshi & Romero 1995, Collins et al. 1996, Robinson et al. 2007). Thus, it is expected that interspecific competition between intertidal bioengineer species will play a significant role in the recovery process of intertidal communities after a strong perturbation.

Perumytilus purpuratus (Lamarck, 1819) and *Semimytilus algosus* (Gould, 1850) are 2 bioengineer mussel species that inhabit the intertidal zone in Chile, with *P. purpuratus* dominating the mid intertidal

level and *S. algosus* the low intertidal level (Fernández et al. 2000, Prado & Castilla 2006). *Perumytilus purpuratus* inhabits the Pacific coast between Ecuador and the Magellan strait, Chile, and around to the southern Atlantic coast of Argentina (Zagal & Hermosilla 2001). This species is one of the strongest competitors in the intertidal zone, outcompeting many other sessile species (Castilla & Durán 1985, Paine et al. 1985, Durán & Castilla 1989, Navarrete et al. 2005). As a bioengineer, this species forms a multiple layer matrix sheltering a high number of organisms and determining the structure of Chilean intertidal communities (Prado & Castilla 2006, Lee & Castilla 2012). *S. algosus* inhabits the coast from Ecuador to the Gulf of Arauco, Chile (Caro & Castilla 2004). Adults are only observed in the low intertidal zone, forming beds composed of a monolayer matrix (Caro & Castilla 2004, Caro et al. 2008), although small individuals (<8 mm) may also be observed within *P. purpuratus* beds in the mid intertidal zone (Caro & Castilla 2004, Caro et al. 2008). Both species exhibit external fertilization with a planktonic larva with a high dispersal potential (Briones et al. 2013).

On 27 February 2010, the south-central coast of Chile was struck by a mega-earthquake and tsunami (8.8 on the Richter scale). The earthquake produced a strong deformation of the coastline near to the epicenter (Vargas et al. 2011). Field observations showed a co-seismic uplift of the coast, reaching more than 3 m with respect to sea level in some areas, causing local extinctions of the intertidal biota (Castilla et al. 2010, Jaramillo et al. 2012). More specifically, at Punta Hualpen in south-central Chile, the uplift produced an extreme mortality of the intertidal biota, especially the 2 mussel species *P. purpuratus* and *S. algosus*, releasing an extensive area of substrate in the intertidal (Fig. 1). Approximately 1 yr after the perturbation, *S. algosus* colonized the impacted area of Punta Hualpen, dominating the mid and low intertidal zones (A. Brante pers. obs.). Over the following months, *P. purpuratus* recolonized the area, forming small patches within the *S. algosus* bed in the mid intertidal zone. The main objectives of the present study were to evaluate the ecological recovery of the populations of *P. purpuratus* and *S. algosus* after the Chilean mega-earthquake of 2010 and determine the role of interspecific competition as mechanism for re-establishing the vertical distribution of these 2 bioengineer mussels in the intertidal zone. We hypothesized that: (1) given the high dispersal potential of the 2 mussel bioengineer species, they would show high levels of ecological recovery; and (2) given the high competitive ability of *P. purpu-*



Fig. 1. Punta Hualpen ($36^{\circ} 46' S$, $73^{\circ} 12' W$), on the central coast of Chile, approximately 7 mo after the mega-earthquake. An uplift of approximately 1 m occurred in this zone. (A) Panoramic view of the former mid intertidal zone. (B) Close-up of empty shells of *Perumytilus purpuratus* killed by desiccation. (C) Mats of *P. purpuratus* byssus threads in zones inhabited by this species before the perturbation

*ratu*s, this species would competitively exclude *S. algosus* from the mid intertidal zone, re-establishing the intertidal distributional patterns of both species observed before the mega-earthquake.

MATERIALS AND METHODS

Perturbation and recovery of the distributional pattern of *Perumytilus purpuratus* and *Semimytilus algosus*

To evaluate the recovery dynamics of both mussel species after a megaperturbation, the temporal changes in abundance and distributional pattern were recorded in the intertidal zone before and after the mega-earthquake. We benefited from yearly surveys carried out by our research team in the highly impacted Natural Sanctuary of Punta Hualpen ($36^{\circ} 46' S$, $73^{\circ} 12' W$; Fig. 2) from May 2009 (1 yr before the perturbation) to December 2013. We carried out periodical studies in this area given its high ecological importance as a Natural Sanctuary. For each survey, the intertidal zone was divided into 2 levels: (1) the low intertidal level, from the area between the *Lessonia spicata* belt (~ 0.2 m mean low water [MLW]) and the *P. purpuratus* belt (~ 0.8 m MLW) and (2) the mid intertidal level, the whole *P.*

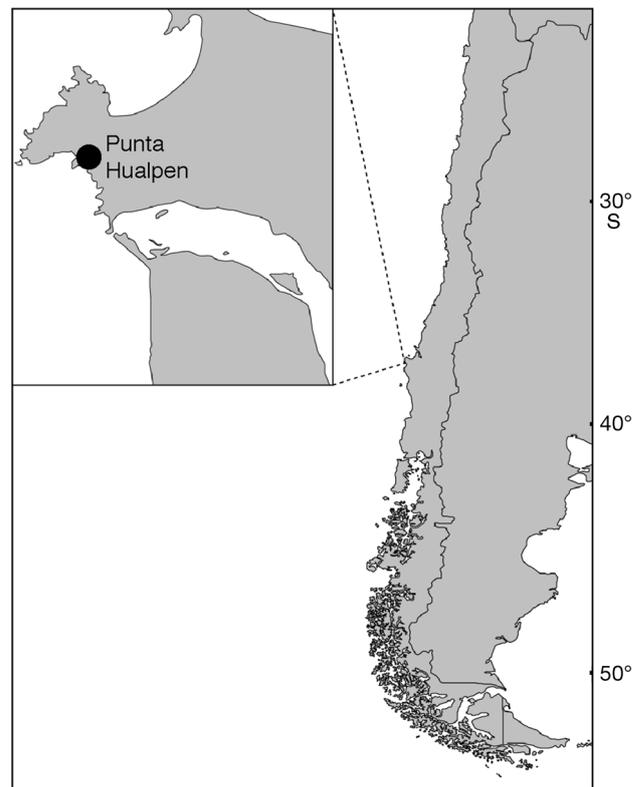


Fig. 2. Field experiments and collection of mussels were carried out at Punta Hualpen ($36^{\circ} 46' S$, $73^{\circ} 12' W$), on the central coast of Chile

purpuratus belt (~between 0.8 and 1.4 m MLW). This zonation is the typical pattern observed on central Chilean rocky intertidal shores (e.g. Broitman et al. 2001). As the zonation pattern was distorted after the perturbation, the different zones were redefined following the same tidal levels used before (low level: 0.2–0.8 m; mid level: 0.8 and 1.4 m MLW). Ten 50 × 50 cm quadrats with 100 points were haphazardly distributed in each intertidal level. Surveys were carried out during May 2009, June 2010, August 2011, May 2012 and December 2013.

Field experiments: temporal evaluation of abundance in patches with different relative dominances of *P. purpuratus* and *S. algosus*

To follow temporal changes in abundance of both mussel species in the mid intertidal zone of Punta Hualpen (36° 46' S, 73° 12' W; Fig. 2) for the 2 yr after the earthquake, plots with the following percentage covers were selected and monitored in the field: (1) those dominated by *P. purpuratus* (70–80% cover); (2) those dominated by *S. algosus* (70–80% cover); and (3) those with a similar cover of both species (~50% cover). In all cases, the initial percent cover of mussel was 100% (no primary substratum available). We monitored a total of fifteen 20 × 20 cm plots (5 replicates per initial abundance condition) haphazardly distributed in the mid intertidal zone for 10 wk between May and July 2012. Plots were marked in each corner with small pieces of epoxy putty and a unique number was assigned to each plot. The distance between plots was at least 1 m. Percentage cover of both mussel species was determined with a quadrat of 400 points every other week. At the end of the survey period, the rate of change in the percentage cover was estimated for each plot using the following formula: (initial cover–final cover)/initial cover. Negative values indicate a decrease in percentage cover.

Laboratory experiments: effect of the competitive interaction between *P. purpuratus* and *S. algosus* on survival and growth rates

During low tides in May 2012, individuals of both species were collected from the mid intertidal zone of Punta Hualpen and transported to the Marine Biology Station Abate Juan Ignacio Molina of the Universidad Católica de la Santísima Concepción. In the laboratory, valve length was measured and used to

divide the mussels into 2 size categories: (1) small body size (SBS; 8–9 mm) and (2) large body size (LBS; 25–27 mm).

We evaluated the effects of interspecific competition on 2 fitness traits, survival and growth rates, of *P. purpuratus* (Pp) and *S. algosus* (Sa) in both size categories. Three experiments were performed. The first showed an SBS–SBS interaction. Thirty small mussels forming experimental clumps were assembled to generate 4 different treatments: (1) dominance of *P. purpuratus* (Pp > Sa), 20 Pp and 10 Sa; (2) dominance of *S. algosus* (Pp < Sa), 10 Pp and 20 Sa; (3) without dominance (Pp = Sa), 15 individuals of each species; and (4) control (no interspecific competition), 30 individuals of each species were cultivated separately. The second experiment involved an LBS–LBS interaction. The same 4 combination treatments described above were performed with large individuals. And the third was an SBS–LBS interaction. Twenty individuals were arranged to generate 3 treatments: (1) 10 small Pp and 10 large Sa; (2) 10 small Sa and 10 large Pp; and (3) 20 small and large individuals of each species were cultivated separately (control treatment). According to many authors (e.g. Cousens & O'Neill 1993, Jolliffe 2000, Shinen & Morgan 2009), replacement series-type designs, such as the one we used in the present study, are valuable especially when field and laboratory species responses are consistent. Experiments were monitored for 70 d, and mortality was recorded every second day. At the end of the experiments, the valve lengths of surviving individuals were measured to estimate growth rate (mm d⁻¹). A total of 5 replicates (experimental clumps) per treatment were used.

For the assemblage of experimental clumps, individuals were kept together over the first 5 d by a plastic net glued to the bottom of a plastic box to promote attachment of the byssus threads of individuals (one plastic box per clump). The size of each clump was approximately 5 × 5 cm for the smaller body size category and 10 × 10 cm for the larger size category. To simulate natural conditions of the mid intertidal zone, all experiments were performed under an artificial tidal regimen using an electric valve connected to a timer, which allowed for the filling and draining of trays where the experimental clumps were maintained. To allow water to flow through the plastic boxes, holes were drilled in their sides. Tidal immersion and emersion alternated every 6 h. During immersion, unfiltered seawater pumped directly from the sea in front of the laboratory was used in all experiments with a temperature of approximately 13°C and a salinity of 35 ppm. This ensured natural

seston food availability during high tides for all clumps. During the emerged periods, individuals were exposed to a room temperature of approximately 17°C.

Statistical analyses

The rate of change in cover of both mussel species in field experiments was compared using a 2-way ANOVA with 2 fixed factors: species (*P. purpuratus* and *S. algosus*) and initial coverage ($P_p > S_a - P_p < S_a - P_p = S_a$).

Given that survival of small individuals of *P. purpuratus* in the SBS-SBS interaction experiment was 100% in all treatments (see 'Results'), 1-sample *t*-tests were performed to compare the survival of small individuals of *S. algosus* with a fixed value of 100% for each treatment. In addition, a 1-way ANOVA was performed to compare the percentage survival of *S. algosus* between treatments. For the other experiments, 2-way ANOVAs with species and relative abundance as fixed factors were used to compare mean survival and growth rate between treatments. When significant differences were detected, a *posterior* Tukey tests were performed. Prior to analyses, normality and homoscedasticity assumptions were tested. The statistical package STATISTICA 7.0 was used for all analyses.

RESULTS

Perturbation and recovery of the distributional pattern of *Perumytilus purpuratus* and *Semimytilus algosus*

In the mid intertidal zone, cover of *P. purpuratus* was approximately 80% before the mega-earthquake, while *S. algosus* achieved less than 5% cover (Fig. 3). After the earthquake and the coastal uplift had occurred (February 2010), a high mortality of the intertidal biota was observed, leaving a high proportion of bare rock. Four months after the perturbation,

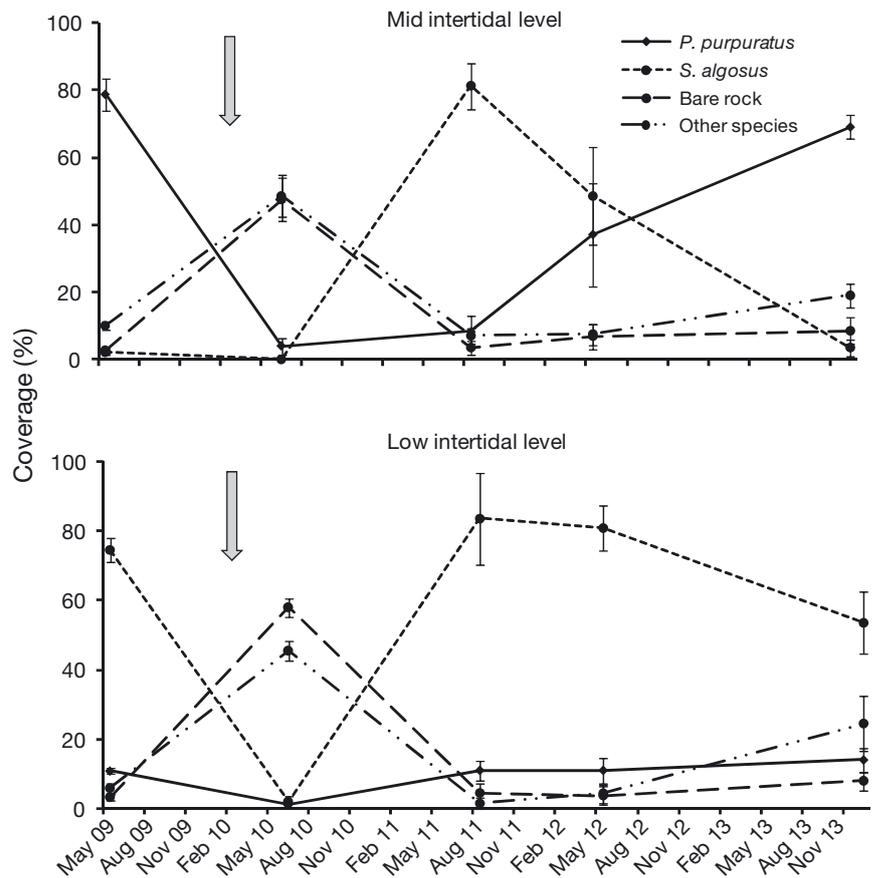


Fig. 3. Temporal evolution of coverage (%) of *Perumytilus purpuratus*, *Semimytilus algosus*, bare rock and other species at Punta Hualpen, Chile, in the mid and low intertidal zones before and after the mega-earthquake of 27 February 2010 (gray arrows). Data are means \pm SE of ten 50 \times 50 cm quadrats with 100 points

an average of 18% of the substrate was covered by ephemeral green algae, such as *Enteromorpha* sp., *Ulva* sp. and species of *Porphyra*. By the middle of 2011, a high abundance of the mussel *S. algosus* was recorded, reaching approximately 80% cover, which then decreased by 2013 to be replaced mainly by *P. purpuratus* and, to a lesser extent, other species (Fig. 3). By the end of 2013, *P. purpuratus* achieved levels of cover similar to those prior to the mega-earthquake.

Similar temporal trends were observed in the low intertidal zone over the first 2 yr: high mortality of mussels, denudation of the rock and settlement of *S. algosus* (Fig. 3). In addition, a few holdfasts of the brown algae *Lessonia spicata* survived the uplift. *S. algosus* persisted in this zone over the following years at levels similar to those recorded before the earthquake, while *P. purpuratus* never achieved more than 15% cover on average (Fig. 3).

Field experiments: temporal evaluation of abundance in patches with different relative dominances of *P. purpuratus* and *S. algosus*

The temporal monitoring of the cover of both mussel species in the field showed that although *P. purpuratus* increased its abundance in all of the initial abundance conditions evaluated, coverage of *S. algosus* decreased (Fig. 4). In all cases, bare substrate did not exceed 15% (Fig. 4). The 2-way ANOVA on the coverage change rate showed significant differences in the interaction term (species \times relative coverage, 2-way ANOVA: $F_{2,24}=13.74$, $p < 0.001$). As a general pattern, the Tukey *a posteriori* test indicated that *P. purpuratus* exhibited the highest positive changes in cover in contrast to the negative and significant values observed in the cover of *S. algosus* in all treatments ($p < 0.05$).

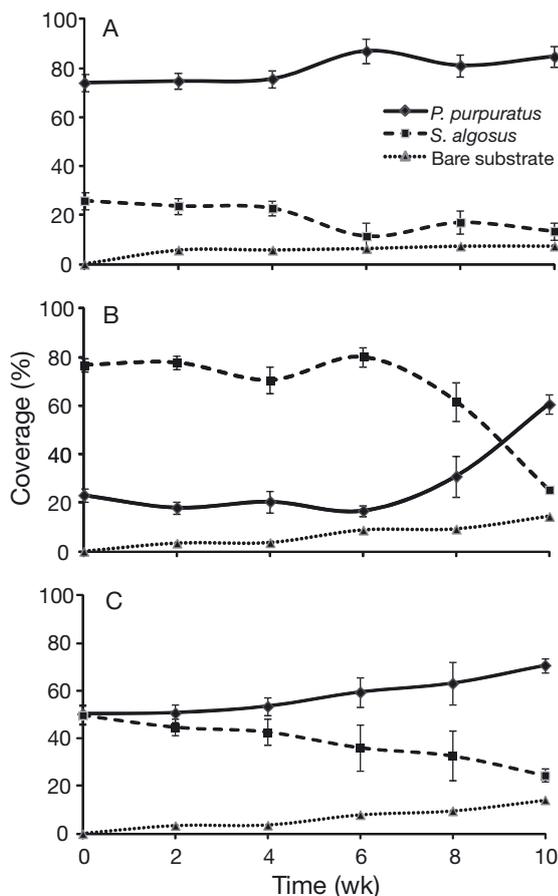


Fig. 4. Temporal evolution of coverage (%) of *Perumytilus purpuratus* and *Semimytilus algosus* in 20 \times 20 cm plots arranged in 3 different initial abundance conditions: (A) higher coverage of *P. purpuratus* (70–80%); (B) higher coverage of *S. algosus* (70–80%); and (C) similar coverage of both species (~50%). Data are means \pm SE of 5 replicates (plots) per treatment

Laboratory experiments: effect of the competitive interaction between *P. purpuratus* and *S. algosus* on survival and growth rates

SBS–SBS interaction

Percent survival of small individuals of *P. purpuratus* was 100% in all treatments (Pp > Sa, Pp < Sa, Pp = Sa, controls), indicating no effect of the presence of *S. algosus* in the clump. By contrast, 100% of survival of *S. algosus* was observed in the control treatment (*S. algosus* only), but the presence of *P. purpuratus* negatively affected the survival of this species, causing it to decrease to 84 and 89% on average (Fig. 5A). Given that survival was 100% and no variance was obtained for *P. purpuratus* and for the control in *S. algosus*, survival means of *S. algosus* for all treatments interacting with *P. purpuratus* were compared with a theoretical value of 100 using a 1-sample *t*-test. Results showed that the percent survival of *S. algosus* was significantly lower than 100% when *P. purpuratus* co-occurred in a clump, in all relative proportion treatments tested (Pp > Sa: $t = -3.14$, $gl = 4$, $p < 0.05$; Pp < Sa: $t = -3.54$, $gl = 4$, $p < 0.05$; Pp = Sa: $t = -3.67$, $gl = 4$, $p < 0.05$). In addition, no differences in the mean survival of *S. algosus* were observed between treatments in the presence of *P. purpuratus* (1-way ANOVA: $F_{2,12} = 0.33$, $p = 0.72$).

The 2-way ANOVA of the growth rate of smaller individuals showed significant differences in the interaction term (species \times relative abundance, ANOVA: $F_{3,32} = 3.26$, $p = 0.03$; Fig. 5B). The general pattern after the *a posteriori* Tukey test showed that the growth rate of small individuals of *S. algosus* was negatively affected by the presence of *P. purpuratus* in the clump in all treatments compared to the control (Fig. 5B). By contrast, except for the treatment where *S. algosus* had a higher percentage cover, no significant effect of *S. algosus* on growth rate of *P. purpuratus* was observed (Fig. 5B). Growth rate of the smaller individuals did not differ in the control treatments between species.

LBS–LBS interaction

Survival of large individuals of *P. purpuratus* ranged from 84 to 93% for all treatments (Fig. 6A). Survival of *S. algosus* was lower than the survival of *P. purpuratus* in all cases, except for the control treatment, oscillating between 52 and 91% (Fig. 6A). Significance in the interaction term was detected for this trait (species \times relative abundance, ANOVA: $F_{3,32} =$

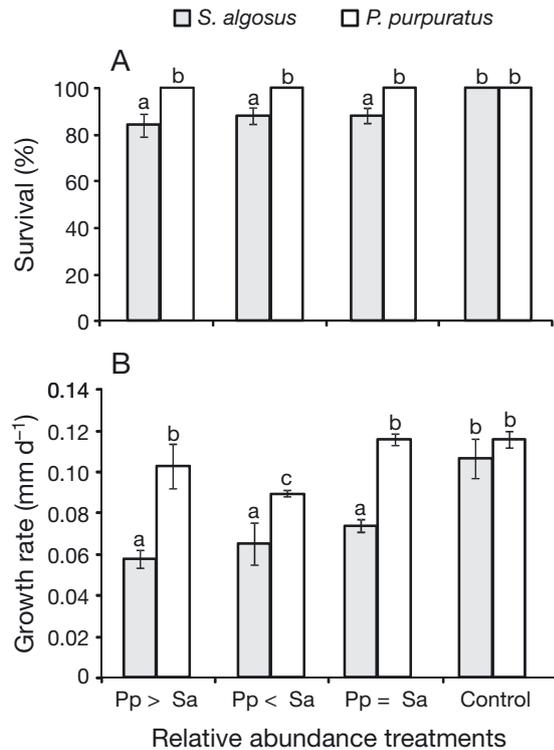


Fig. 5. Laboratory performance of 2 fitness traits of small individuals of *Perumytilus purpuratus* (Pp) and *Semimytilus algosus* (Sa) in forced coexistence conditions: (A) survival rate and (B) growth rate. Experimental clumps were constructed with a total of 30 ind. arranged in 4 treatments: (1) dominance of *P. purpuratus* (Pp > Sa): 20 ind. of Pp and 10 ind. of Sa; (2) dominance of *S. algosus* (Pp < Sa): 10 ind. of Pp and 20 ind. of Sa; (3) without dominance (Pp = Sa): 15 ind. of each species; and (4) control (without interspecific competition): 30 ind. of each species cultivated alone. Data are means \pm SE of 5 replicates (clumps) per treatment. Different lower-case letters indicate significance at $p < 0.05$

4.51, $p < 0.001$). The Tukey *a posteriori* test showed that survival of larger individuals of *S. algosus* was negatively affected by the presence of *P. purpuratus* in the clump in all treatments compared with the control (Fig. 6A). By contrast, survival of larger individuals of *P. purpuratus* was not affected by the interaction with *S. algosus* in the clump (Fig. 6A). No significant differences were observed in the control treatments between species.

Growth rates of large individuals differed only between species (ANOVA: $F_{3,32} = 3.98$, $p < 0.01$; Fig. 6B). In contrast to the smaller size category, the Tukey *a posteriori* test suggested that large *P. purpuratus* exhibited higher growth rates than large *S. algosus* in the control treatment. In addition, *S. algosus* showed lower growth rates in the presence of *P. purpuratus* in all of the abundance combinations assayed (Fig. 6B).

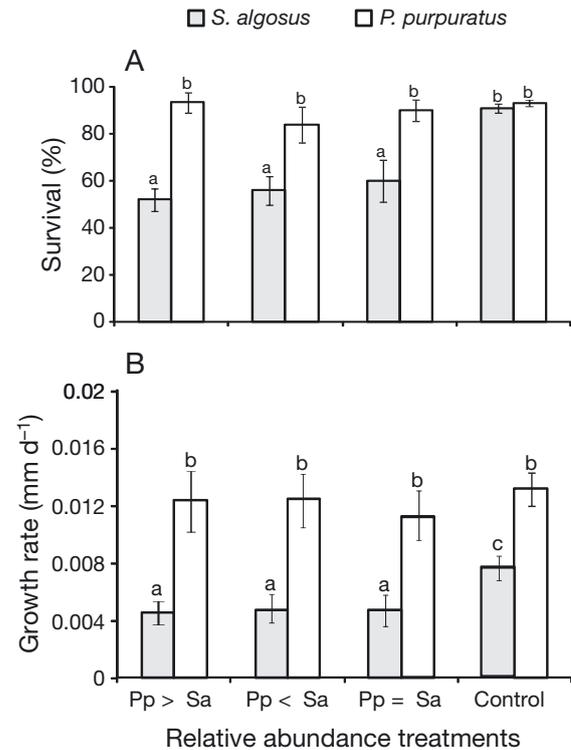


Fig. 6. Laboratory performance of 2 fitness traits of large individuals of *Perumytilus purpuratus* (Pp) and *Semimytilus algosus* (Sa) in forced coexistence conditions: (A) survival rate and (B) growth rate. Experimental clumps were constructed with a total of 30 ind. in 4 treatments: (1) dominance of *P. purpuratus* (Pp > Sa), 20 ind. of Pp and 10 ind. of Sa; (2) dominance of *S. algosus* (Pp < Sa), 10 ind. of Pp and 20 ind. of Sa; (3) without dominance (Pp = Sa), 15 ind. of each species; and (4) control (without interspecific competition), 30 ind. of each species cultivated alone. Data are means \pm SE of 5 replicates (clumps) per treatment. Different lower-case letters indicate significance at $p < 0.05$

LBS–SBS interaction

Mean survivorship of large and small individuals of *P. purpuratus* cohabiting with *S. algosus* ranged between 96 and 99% in all treatments (Fig. 7A). In contrast, mean survivorship of *S. algosus* for both ontogenetic stages oscillated between 68 and 91%, with the highest value observed in the control treatment (*S. algosus* alone). The 2-way ANOVA showed a significant interaction between species and ontogenetic stage (ANOVA: $F_{3,32} = 10.2$, $p < 0.001$). The *a posteriori* Tukey test indicated that, in general, survivorship of *P. purpuratus* did not differ between treatments ($p > 0.05$) and was significantly higher than that observed for *S. algosus* under all ontogenetic stage combinations, except for the control treatments, where survival did not differ between species

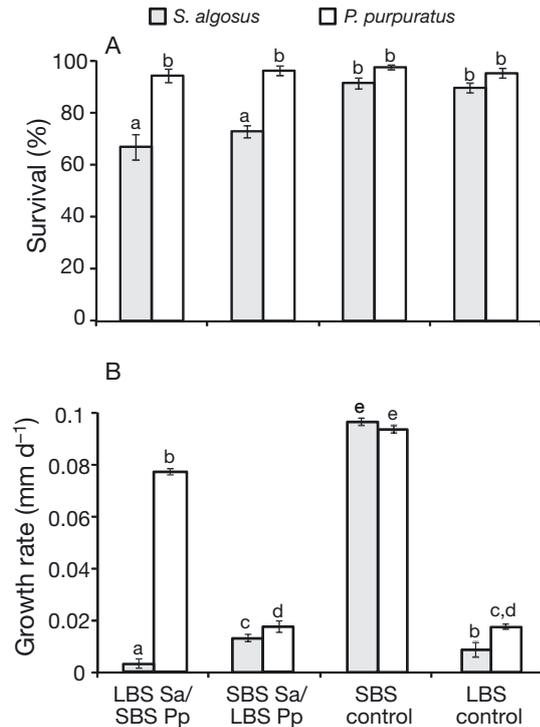


Fig. 7. (A) Survival rate and (B) growth rate of *Perumytilus purpuratus* (Pp) and *Semimytilus algosus* (Sa) were measured in experimental clumps combining small and large individuals in 4 treatments: (1) 10 ind. of large body size (LBS) Sa and 10 ind. of small body size (SBS) Pp; (2) 10 SBS Sa and 10 LBS Pp; and (3) 20 SBS and (4) 20 LBS of each species cultivated alone (control treatment). Data are means \pm SE of 5 replicates (clumps) per treatment. Different lower-case letters indicate significance at $p < 0.05$

($p > 0.05$; Fig. 7A). Similarly, no differences were detected between treatments for *S. algosus* ($p > 0.05$), except the control treatment, which exhibited higher survival ($p < 0.05$; Fig. 7A).

For growth rate, the 2-way ANOVA was significant for the interaction term species \times ontogenetic stage ($F_{3,32} = 6.2$, $p = 0.002$; Fig. 7B). The Tukey test showed that the growth rate of *P. purpuratus* was generally unaffected or less affected by the presence of species other than *S. algosus* at all ontogenetic stages. In the combination of large individuals of *S. algosus* and small individuals of *P. purpuratus*, growth rate significantly decreased in both species with respect to the controls ($p < 0.05$); however, while mean growth performance of small individuals of *P. purpuratus* decreased by approximately 30%, growth rates of large individuals of *S. algosus* were reduced by almost 60% in comparison with the controls (Fig. 7B). When small individuals of *S. algosus* and large individuals of *P. purpuratus* were present in the same clump, growth rates of small individuals of *S. algosus* de-

creased significantly ($p < 0.05$), by more than 80% on average with respect to the control (Fig. 6B). By contrast, growth rates of large individuals of *P. purpuratus* did not differ significantly from those of the controls ($p > 0.05$; Fig. 7B).

DISCUSSION

The mega-earthquake that struck south-central Chile in 2010 produced important changes in the geomorphology of the coast. These changes dramatically affected the community structure of coastal biota, producing in some cases massive local extinctions (Castilla et al. 2010, Jaramillo et al. 2012). Prior to the earthquake, the intertidal bioengineer mussels *Perumytilus purpuratus* and *Semimytilus algosus* exhibited a structured distributional pattern, with the former dominating the mid intertidal zone and the latter the lower intertidal zone. At Punta Hualpen, the coastal uplift after the earthquake produced massive mortality of both species, which had a significant impact on the biodiversity of the intertidal zone. However, our main findings suggest that intertidal communities affected by the mega-earthquake on 27 February 2010 have a great potential for ecological recovery. Moreover, the high dispersal potential of both species and the lower competitive ability of *S. algosus* with respect to *P. purpuratus* may explain the recovery pathway and the ecological recovery capacity of intertidal communities in south-central Chile.

After the massive mortality of the intertidal biota and the clearing of the substrate due to the uplift of the coast, ephemeral green algae were the first organisms to arrive, covering a high proportion of the substrata by the end of 2010. In fact, in the field survey of June 2010, 80% of the 'other species' category (Fig. 3) corresponded to *Ulva* sp. and *Enteromorpha* sp. After that, recruitment of mussels was observed. Usually, larvae need specific chemical cues or specific microhabitats in order to settle. For example, laboratory studies have shown that algal chemical cues promote metamorphosis and settlement in marine invertebrates (Dobretsov & Qian 2003, García-Lavandeira et al. 2005, Alfaro et al. 2006). Alternatively, macroalgae may provide a filamentous matrix that facilitates larval settlement (Beckley 1979, Petersen 1984, Lasiak & Barnard 1995, Moreno 1995, Littorin & Gilek 1999, Erlandsson & McQuaid 2004). Thus, it is possible that the delayed arrival of mussel species observed in the study area may be related to the earlier arrival of green algae and then the appearance of suitable substrata or microenvironments for settlement.

Field observations showed that *S. algosus* was the first mussel species to arrive in the impacted zone, with high abundances in the field survey in August 2011 in the mid and low intertidal zones. In the same year (2011), *P. purpuratus* recruited on the *S. algosus* bed in the mid intertidal zone with low abundances, but increased in abundance through to 2013. Previous work carried out on the central coast of Chile has shown that recruitment occurs throughout the year in both species, with a peak during the austral spring–summer months for *P. purpuratus* and austral winter for *S. algosus* (González et al. 1980, Lagos et al. 2007, Navarrete et al. 2008). In addition, sexually mature individuals may be observed year round in both species in south-central Chile, with 3 reproductive peaks for *P. purpuratus*, February, July, and between October and November (austral spring), and 2 peaks for *S. algosus*, between March and April (austral autumn), and between September and October (austral spring) (González et al. 1980). These observations indicate that at the time of our experiments (between May and December 2013), at least 3 peaks of recruitment for both species occurred after the mega-earthquake. It is possible that the first arrival of *S. algosus* observed at Punta Hualpen may be explained by the winter spawning of 2010.

After the establishment of *S. algosus* from the mid to low intertidal zone, *P. purpuratus* arrived on the *S. algosus* bed. Facilitation mechanisms between mussel species have been reported previously. For example, *Perna perna* improves the survival of *Mytilus galloprovincialis* in the short term in mixed patches but excludes it competitively in the longer term (Rius & McQuaid 2006, 2009). The spring–summer reproductive peak of *P. purpuratus* mainly at the end of 2011 allowed larvae of this species to recruit onto adult *S. algosus* beds. The matrix formed by *S. algosus* may have provided the appropriate habitat for *P. purpuratus* larvae recruitment at the early stage of ecological succession, allowing them to establish.

A wide area of the south-central coast of Chile suffered a surface deformation during the 27 February 2010 mega-earthquake (Vargas et al. 2011). However, some coastal areas were unaffected and the intertidal biota remained unimpacted (Vargas et al. 2011). Larval bivalves spend between 2 and 5 wk in the water column (Ramorino & Campos 1979, Gosling 2003), allowing population connectivity at small and meso spatial scales. Although we do not have information for *S. algosus*, larvae of *P. purpuratus* spend approximately 14 d in the plankton (Ramorino & Campos 1979). Population genetics analyses for *P. purpuratus* on the north-central coast of Chile have

shown highly connected populations at the scale of hundreds of kilometers (Briones et al. 2013). Specific life history strategy characteristics, such as the presence of an intermediate dispersal stage, may facilitate the arrival of propagules in impacted areas from undisturbed populations through source–sink dynamics, promoting ecological recovery. In addition, as *P. purpuratus* and *S. algosus* are 2 important ecosystem bioengineers forming 3-dimensional microhabitat matrices, their establishment promotes the arrival of other important components of the intertidal community such as crabs, polychaete worms, other mollusks, meiofauna and seaweeds (Prado & Castilla 2006, Kelaher et al. 2007, Lee & Castilla 2012), favoring the ecological recovery process.

A fast replacement of *S. algosus* by *P. purpuratus* in the mid intertidal zone was observed 18 mo after the perturbation. Food and space availability are the main limiting resources for sessile organisms in the intertidal zone, especially for sessile and sedentary organisms with aggregated distributions (Connell 1961, Harger 1968, Dayton 1971, Menge & Sutherland 1976). *P. purpuratus* and *S. algosus*, like other filter-feeding sedentary species, compete for sestonic food and attachment substrate (Frechette & Despland 1999, Shinen et al. 2009). Interspecific competition may play an important role in growth and mortality in the distribution of the mussels *Mytilus edulis* and *M. californianus* (Harger 1968). As a general pattern, our laboratory experiments indicated that *S. algosus* was negatively affected by the presence of *P. purpuratus*. Growth rates and survivorship of *S. algosus* in both body size categories (small and large) were lower when they were cultivated with *P. purpuratus*. Similarly, when experimental clumps were composed of individuals of both species at different ontogenetic stages (sizes), irrespective of the species–ontogenetic stage combination, *S. algosus* exhibited lower survival and growth rates with respect to the control treatment. These observations suggest that the lower competitive ability of *S. algosus* with respect to *P. purpuratus* may explain the decreasing trend in abundance of *S. algosus* in the mid intertidal zone observed in the field.

The experiments did not allow us to directly differentiate between interspecific competition by interference and exploitation mechanisms. However, some lines of evidence suggest different mechanisms of competition operating at early and late ontogenetic stages. First, *P. purpuratus* and *S. algosus* exhibited similar growth rates in the smaller size category in the control treatment (0.11 mm d^{-1} on average). In contrast, higher growth rates were observed in large

individuals of *P. purpuratus* (0.013 mm d^{-1}) in comparison with large individuals of *S. algosus* (0.008 mm d^{-1}). Similar trends in growth rates have been reported for both species and for other intertidal mussels (González et al. 1980, Cancino & Rojas 1986, Shinen et al. 2009). The better growth performance of large individuals of *P. purpuratus* in comparison with *S. algosus* may suggest a higher exploitation efficiency through clearance rate by filtration in *P. purpuratus*. Studies in adult individuals of the successful mussel invader *M. galloprovincialis* suggest that exploitation throughout clearance rate efficiency might be an important mechanism of competition in this species, displacing other mussels from their native habitat (Griffiths et al. 1992, Hilbish et al. 1994, Shinen et al. 2009). Although we do not have an extensive experimental evaluation of the clearance rate of both species at different ontogenetic stages, preliminary observations on a few individuals suggest that *P. purpuratus* has a higher clearance rate than *S. algosus*, with values around 250 and 50 $\text{ml h}^{-1} \text{ ind.}^{-1}$, respectively. Furthermore, growth rate and survival of smaller individuals of *P. purpuratus* were not affected by larger individuals of *S. algosus*, for example, by the 'shading effect'. More detailed observations on the configuration of experimental mussel clumps showed that smaller individuals of *P. purpuratus* are located on top of the shells of *S. algosus*, reducing or eliminating the shading effect. Differences in motile and aggregation behavior have been reported in other mussels (Shinen et al. 2009). For example, while *Mytilus galloprovincialis* and *M. californianus* are less mobile, *M. trossulus* dispersed from mussel clumps more frequently and over greater distances (Shinen et al. 2009). Harger (1968) suggests that highly mobile behavior in mussels may confer significant advantages in crowded habitats, where moving above competitors or to unoccupied substrate may prevent suffocation or increase food intake. Both observations suggest that, although our experiments were conducted over a short time scale (70 d), exclusion of *S. algosus* by *P. purpuratus* from the mid intertidal zone may be explained by a combination of interspecific competition by interference when they are small and competition by exploitation at larger body sizes. More laboratory experiments on clearance rates and movement behavior of individuals within patches of *P. purpuratus* and *S. algosus* at different ontogenetic stages are needed to test these hypotheses.

Contrary to observations in the mid intertidal zone after the perturbation, *S. algosus* recruits and persists at a high abundance in the low intertidal level, establishing a dense monospecific belt, similar to that ob-

served before the mega-earthquake. Previous research has shown that intertidal bivalves in general, and *P. purpuratus* specifically, exhibit higher growth rates (corrected by submersion time) at intermediate tidal heights than at lower tidal heights or subtidally (Gillmor 1982, Cancino & Rojas 1986). In addition, during our periodic sampling in the experimental area, recruits (~1 mm length) of *P. purpuratus* were observed throughout the year within the *S. algosus* matrix in the low intertidal zone. This observation agrees with other reports for the intertidal in central Chile in which a constant recruitment with a peak during austral summers has been observed for *P. purpuratus* (Navarrete et al. 2008). In fact, small patches of adult *P. purpuratus* were observed before and 18 mo after the mega-earthquake, oscillating around 10% cover (Fig. 3), suggesting no limitation by larvae recruitment. Although we do not have data on the performance of *S. algosus* at different tidal levels, these observations suggest that *S. algosus* is a better competitor at lower intertidal heights, outcompeting *P. purpuratus* in this zone.

The 27 February 2010 mega-earthquake that struck south-central Chile produced important changes in the intertidal ecosystem, causing massive local extinctions over a large coastal area. Two years after the perturbation, intertidal habitats showed important signs of ecological recovery, with the establishment of the 2 most important bioengineer intertidal species, the mussels *P. purpuratus* and *S. algosus*. Life history strategies such as a high dispersal potential due to the existence of an intermediate free-living stage and differences in competitive abilities could explain the ecological recovery of both species after the mega-earthquake and the different intertidal vertical distributional patterns of both species. Large-scale temporal monitoring is needed to determine whether this first step in ecological recovery can re-establish the diversity and structure of the entire coastal community.

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